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Reasoning an appendicular and functional caddisfly genital terminology

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Mating structures have long been of interest to taxonomists because of their utility in distinguishing between species. Insect genitalia indeed vary more from species to species than do legs, wings, cephalic or thoracic structures providing a powerful tool for species-level taxonomy. Genital segments and their appendages play a major role in caddisfly taxonomy and are widely used to discriminate between species. Good genital drawings give focused identity images of species. However in the text of species descriptions we need to apply an updated homologous genital terminology, in spite of the possible misuses due to unresolved difficulties in homologising the particular structural elements of the insect genitalia. Even if we succeed in adopting a homologous genital terminology in the practice of biodiversity quantification, and apply the template principle in species description (EVENHUIS, 2007), the replacement of morphospecies with taxonomic species of alpha taxonomy remains a resource intensive task. Governments need a new financial policy for grant allocation, in order to realise a combined effort of several approaches answering questions in resource quantification. (1) Why is species description so vital for human survival? We need to quantify the declining biodiversity resources. We need to measure and calculate the financial value of ecosystem services with eco-eco procedures. (2). Why are the male genitalia so diverse? We need to study the evolution of genital diversity in sexual selection. (3) Why is an appendicular and functional genital terminology more promising? We need to target a more homologous appendicular terminology for species description. This would help us to utilise comparative phylogeny for higher level taxonomy and would contribute to the understanding of functional and historical relations in biodiversity resource production and consumption. Here we present our learning and understanding on these questions. For those who are engaged simply in species descriptions, we include here an interim list of the genital terms we have collected recently as a practical annotation during our species descriptions in *Psychomyioidea*, *Hydropsychoidea* and *Leptoceroidea* superfamilies.

Why is species description so vital?

Species form the biodiversity, the resources of ecosystem services. It functions like a global commercial bank producing the life-supporting ecosystem services as well as like a huge insurance bank ensuring its long-term viability. The economic valuation of ecosystem services produced by the biodiversity resource became a promising interdisciplinary research area in recent years. We are becoming more aware that only a small fragment of the biodiversity resource is described, and running with time in the vital process of revising the neoliberal economic ideas that kill our living companies, while degrading biodiversity resources in an accelerating rate. How can we survive the dictates of the "Modern Economic Man"? Why is this biodiversity crisis so vital? Why do we need to quantify the biodiversity with species survey and description? Are we able to describe the unknown species even if the present funding scenario changes and becomes linked to describing new species (FLOWERS, 2007)? Lack of taxonomists to handle the task of identifying and naming undescribed species, that is

the lack of expertise to effectively describe the remaining biodiversity on earth is a real "taxonomic impediment" (HOAGLAND, 1996). Is it really an impediment or is it rather an expedient (WHEELER et al. 2004)? There is "another taxonomic impediment" (EVENHUIS, 2007) that is clearly an expedient. That is simply our inactivity in describing new species and this is created and maintained by our inherent human character that few taxonomists enjoy the entire process in the publishing arena. Individual taxonomists have their own habits. Few of us complete all the eight steps leading to the taxonomic nirvana of species description. Both the limited number and the inactivity of taxonomists contribute to the present scenario when we are unable to keep up the rate of describing over killing. Under the increasing pressure of resource consumption and malfunctioning allocation we are facing the problem of how to describe rapidly and reliably the unknown species. Species which have still survived in the habitat fragments left, and species which have been already extinct but waiting for description as dead specimens in collections. Human ethics, the philosophy of morality urges our human duty to produce at least a monument of description for these tiny creatures, who constitute the biosphere together with us in their own right. Moreover their biodiversity produces annually 180 10^{12} USD, the calculated global value of ecosystem services vital for sustainable economy and for human survival (BOUMANS et al. 2002). This is 4.5 times more than the annual gross world product (GWP: 40 10^{12} USD in 2000) of the "modern economic man".

Why caddisflies?

In these eco-eco surveys the estimation of the intrinsic economic value of ecosystem services powered by water network has attained especially high priority. Several studies have documented that wetland ecosystems have far the highest monetary value of the ecosystem services. The operational capacity of ecosystem services that is the health of any particular ecosystem or any complex of landscapes or landuse pattern to produce these ecosystem services is measured by their ecosystem integrity. This integrity is sampled representatively in carefully selected ecosystems and then quantified by their diversity using only an adequate indicator segment of the total community structure. We need to determine the known, and describe the unknown species of a suitable indicative group of organisms. The quantification of the total diversity is almost impossible. It requires expensive specialists and financial capacity to determine, to describe and to quantify taxonomic species. The old theory or rather a naïve dream to measure and evaluate the diversity integrity of ecosystems with the analysis of their entire community structure has totally failed. Theoretically and practically it is impossible, and even it is not required at least at the landscape resolution level. Depending on the available human, scientific and financial resources it is sufficient to select a locally suitable indicator segment of the total community to quantify the entire integrity of the ecosystems. In our practice the extremely diverse aquatic insect order of Trichoptera offers a simple procedure to estimate the integrity of the running water ecosystems. The integrity of the running water network reflects the integrity of the entire drained landscape. The measured integrity of these flowing waters is the net result of the drained land use activities, so the integrity values quantified for the water network are reasonably extrapolated to the different land use patterns and reliably integrated to the entire landscape. In running waters, the genera of the net-spinning *Hydropsychidae* family are far the most important diversity and biomass components. Besides of their primary involvement as an indicator tool in

measuring the integrity of ecosystem services their net-spinning larvae themselves generate significant ecosystem services by the intensive filter-feeding activity. The surface of their filter retreats with net mesh-size range of 30-600 µm filters and cleans the river water several times. Just a single hydropsychid genus *Cheumatopsyche* may develop a maximal larval population densities of between 1-30 thousands (HYNES 1975, PETR 1970, STATZNER 1982, 1984, BOTOS et al. 1990.) and up to 250 thousands (GIBBS, 1973) individuals per square meter. This large biomass with its filter feeding activity removes huge amount of suspended solids from all kind of running waters, maintaining and enlarging their purification capacity.

Why are male insect genitalia are so diverse?

How can we quantify the biodiversity, other than just morphospecies as surrogates of taxonomic species? How can we describe the unknown species rapidly and reliably for ecosystem integrity survey with limited resources? Male genitalia are extraordinarily diverse in form and function, implying extraordinarily rapid rates of morphological evolution. Three hypotheses have been developed to explain the evolution of male genitalia: the „lock and key”, the „pleiotropy”, and the „sexual selection” hypotheses. (1) Under the lock-and-key hypothesis, selection for preinsemination reproductive isolation is predicted to favour male genitalia, that provides an exact mechanical fit to female genitalia (EBERHARD, 1985). (2) The pleiotropy hypothesis suggests that variation in genitalic morphology is selectively neutral and that male genitalia evolve via pleiotropic effects of genes that code for both genital and general characters (MAYR, 1963). Pleiotropy describes the genetic effect of a single gene on multiple phenotypic traits, signalling function on various targets. Finally, (3) the sexual selection hypothesis proposes that fertilization success is nonrandom with respect to genital morphology (EBERHARD, 1985). Sexual selection occurs if differences among male genitalia are related to sensory manipulation in mating, to the ability of removing rival sperm in sperm competition, to control fertilization in sexual conflict between male and female, and to induce post-copulatory preferential sperm utilization in cryptic female choice (ARNQVIST, 1997).

The lock and key hypothesis

The lock-and-key hypothesis states that genitalia vary between species in order to provide a mechanical reproductive isolation system. Insects with differing genitalia are usually considered as reproductively isolated species. The male genitalia serve as a barrier against cross-copulations between members of two different species, maintaining a preinsemination reproductive isolation that prevent hybridization. The males of a species must have uniquely shaped „key” to match the genital „lock” of the corresponding females. This hypothesis assumes low within-species variability in genital traits. Darwin himself believed that the evolution of reproductive organs was driven by maintenance of species purity. There is strong selection on females to avoid mating with heterospecific males. Females evolve complicated reproductive structures that allow them to discriminate between conspecific and heterospecific males and to avoid heterospecific fertilizations. The occurrence of this process with each speciation event would result in rapid diversification of genitalia across closely related species. If the diversification and elaboration of mating structures results from selection for reproductive isolation, there should be species-specific fits of male and female mating structures. The lock and key hypothesis is popular, but there is little

evidence to support it (MAYR, 1963). Lock and key system diversifies the genital structure of monandrous species, but in nature the polyandrous species are more diverse (ARNQVIST (1997). The lock and key hypothesis is popularly exemplified by the clasper groove and receptacles in *Cheumatopsyche* and *Hydropsyche* species. However male harpagones and female grooves and receptacles do not fit exclusively in many species and this simple mechanical fitting alone does not secure a perfect reproductive isolation (STATZNER, 1974). There are many animals without species-specific fit between male and female mating structures and rapid diversification of genitalia appears to have occurred more in allopatry). If lock and key reproductive isolation works there should be more diversification of mating structures in sympatry than in allopatry (EBERHARD 1985). Nevertheless still we are not ready to throw away the lock and key hypothesis, because it might be achieved through sensory or behavioral fits.

Sexual selection hypothesis

The diversity of insect genitalia is unlikely to have arisen for the simple process of sperm transfer. Genital morphology might be shaped by selection for other functions. Recent studies suggest that the male reproductive organs diversify more in the processes of sexual selection, being equivalent of peacock feathers, bird bower building and deer antlers. Because females of many species mate with multiple partners in polyandry, it is not enough that a male has the key to solicit a copulation. Sexual selection does not stop at attraction, courtship or copulation but continues inside the female and focuses on sperm competition, control fertilization, cryptic female choice, intersex conflict and the polyandry evolution. The race may continue inside the female until the sperm of one male finally succeeds in fertilising eggs. Within the female reproductive tract, there are battles between sperm of different males and differential use of sperm by females. Male must possess features of genitalia that keep and support his sperm in the race of fertilization once mating has occurred. Structural elements on the phallic apparatus work as innervated sensilla or various stimulator and may deliver internal courtship signals to the female, enabling her to assess the quality of the male. ARNQVIST (1997, 1998) has demonstrated that sexual selection drives the genital diversity. The polyandrous and polygamous species have more diverse copulatory organs than monandrous species. Genitalia are conspicuously variable, even in closely related taxa that are otherwise morphologically very similar. Sexual selection is important in driving genital divergence and produced by females on male genitalia. Diversity of male genitalia is the product of competition between individuals of the same species. The post-mating sexual selection theory seems persuasive, and it explains the anomalies that the lock and key hypothesis does not.

There are three possible mechanisms for elaboration of genital structures in sexual selection. (1) Selection of mating structures through mate choice, evolving new male structures through cryptic female choice. Females preferentially use sperm from males sensing characteristics of the male structures and co-selecting females having structures more selective amongst males. (2) Selection of mating structures through intrasexual competition, selecting more effective male reproductive structures to deliver sperm or remove sperm directly/indirectly or otherwise compete with the rival sperms. (3) Selection of mating structures through intersexual conflict over fertilization. Females could be selected to choose sperm of high quality males by various mechanism, for instance by multiple valved spermathecae. Male genital structures could be selected to overcome female choice

mechanisms or to manipulate female behavior by removing sperm of other males from the female reproductive tract. Sexual selection pressure should act again on females to avoid this manipulation in an intersexual arms race. For all the three mechanisms both the periphallallic and phallic organs and structures may serve grasping, clasping and other functions, sensory functions and stimulation functions both in copulation and fertilization. This multiple function produces the high diversity of genital structure of whether appendicular or non-appendicular origin.

Appendicular or non-appendicular?

The difficulties in creating a homology across all the insect orders are produced and maintained by an unresolved debate between two alternative theories existing for the evolutionary origin of insect male genitalia. Whether genital appendages are limb podites or neoformations of sternal evagination? (1) Appendicular theory (SNODGRASS, 1935; SCUDDER, 1971; MATSUDA, 1976) suggests that the male insect genitalia arose through modification from the abdominal segmental appendages of the primitive limb podites and homologous to appendicular elements of the female ovipositor. The phallic organ is fused from the two gonapophyses, the median proximal processes of the coxopodite. The two-segmented gonopod of the periphallallic organ is developed from the coxopodite (gonocoxit), the primary basal segment of the segmental appendages, the primitive limb basis and from the gonostylus the lateral distal process of the coxopodite. (2) Non-appendicular theory (SNODGRASS, 1957) is based on the sternal and mesal evagination (outgrowth) on the ninth abdominal segment associated with the gonopore. According to this theory, two paired lobe-like structure are formed on the ninth segment adjacent to the gonopore already in the larval stage. Two medial lobes, the mesomeres or gonapophyses give rise to the aedeagus and two lateral lobes develop into parameres; parameres are further divided into the basal basimere (gonocoxit) and distal telomere (gonostylus). This theory is supported to some extent by embryonic studies. However ontogenetic studies may be no better an indicator of homology than comparative morphology of the adult structures. Embryonic processes are also subject to selection and modification in evolution just as are the final structures (SCUDDER, 1971). Appendages suppressed in adult may not appear in the embryo. If we apply the non-appendicular theory at least for the holometabolous insects how can we explain the presence of true appendicular structures prevailing at many of the primitive insects and how can we account for the complete disappearance of appendages and of the somites of the postgenital segments. Are they all completely lost, not modified, not fused? Have completely new appendages just appeared (intermediate, superior, preanal) and from where? The old conclusion (MICHENER, 1944) seems more reasonable that the copulatory organs are derived from pre-existing structures of primitive limb podites. It does not seem anymore productive to call the periphallallic organs in neutral terms by anatomical directions just because of trying to escape misuses.

Why appendicular genital terminology?

Very different genital systems have evolved in insects and no single terminology exists applicable across all insect orders. As we have reviewed, one reason for this is that male genitalia are extremely diverse in form and function, with high rates of morphological evolution. Moreover during this process homologous structures may change their functions. The rapid evolution of male genitalia is driven less via lock

and key fit, but mostly via female choice during courtship, copulation and fertilization in the very complex processes of sexual selection. Attempts to establish a single terminology have proven difficult and most of the terminologies used are largely taxon-specific (SNODGRASS, 1935). In caddisflies, the lack of knowledge on plesiomorphic/apomorphic characters, on groundplan and on evolutionary regulating principles of the male genitalia hinders phylogenetic studies and higher taxonomy. Fortunately there is a practical perspective visible already formulated to recognise homologous structures by combined morphological, functional, and historical (fossil) comparative studies in order to establish an appendicular terminology for male terminal segments in Trichoptera (IVANOV, 2005). We believe that Ross's and Nielsen's appendicular terminology based primarily on old arguments of comparative morphology is supported by the new arguments of multiple stimulatory and sensory genital functions generated in recent studies applying the theory of sexual selection. These results give additional details for the functional genital groundplan of the primordial Trichoptera reconstructed from *Amphiesmenoptera* (KRISTENSEN, 1984; SCHMID, 1970, 1989; IVANOV, 2005). The clasping function of the gonopod, the intromittent function of the phallic apparatus, the sensory function of the cercus and the stimulatory function of the paraproct seem to form the basic functional groundplan in male caddisfly genitalia.

Old arguments of comparative morphology

Here we recall the appendicular idea of ROSS (1938) and NIELSEN (1957), and suggest to continue their work to understand the origin and function of the genital segment and appendages and to continue their appendicular terminology. Here is the time to reconsider their movement from directional toward appendicular genital terminology based on comparative morphology of the caddisflies. The directional terminology is neutral and practical, making no scientific challenges to homologisation in species descriptions. This is why it became so popular recently. However as a result we are getting further from understanding homologies of the genital appendages so diversely developed in various taxa. In an universal term, morphology is the science of functioning forms of the ever-changing living or non-living particles and anatomy, and is the human determination of the structural facts. Anatomical directions help us to orientate in the structural diversity like the compass rose on a map. Directions can be used to describe the locations of any structures in relation to other structures or locations in the body. Each directional term often has a counterpart with converse or opposite meaning realising the benefits available in the scientific tool of comparison and can also be applied to the planes of the body. Anatomical directional terms were adopted first by MCLACHLAN (1874-1880) to describe the structural units of the male Trichoptera genitalia: (1) inferior appendages, (2) intermediate appendages, (3) superior appendages. In Europe, these directional terms were kept for a long time (MOSELY, 1939). They were slightly modified by KIMMINS (MOSELY & KIMMINS, 1953), dropping the loosely applied term of intermediate appendages and adapting the term of upper penis cover. Directional terminology was applied by MARTYNOV (1934) and by BETTEN (1934). However they made a step toward appendicular terminology, remarking that the superior appendages are actually anal or preanal appendages and inferior appendages are gonopodes or claspers. ROSS (1938) was the first to use definitely appendicular terminology, relying on the segmental appendages of the primitive limb and applying clasper for inferior appendages and declaring that the superior appendages (preanal appendages, anal appendages, socii) are

indubitably associated with the lateral margin of the tenth tergite. For this reason, they are considered the true cerci and in many of the more primitive genera there are no doubt that these cerci are homologous to the same structure in *Hymenoptera*, *Mecoptera* and other orders. The next important step in appendicular terminology was produced by NIELSEN (1957, 1980). He has completed extensive and sophisticated studies on the comparative morphology of both the male and female genital segments of Trichoptera, including detailed studies on musculature. He demonstrated that intermediate appendages are the modified paraproct complex of the eleventh segment. A more or less distinct segment XI developed only in the *Rhyacophilidae* (SCHMID, 1970) but the paraproctal complex or traces of it can be found in most of the Trichoptera.

The long-lasting influence of the single-sided disputes on genital homologies especially on paraproct versus intermediate appendages (NIELSEN, 1957; SCHMID, 1958, 1970, 1979, 1989, 1998) has inspired further studies, mostly on the phallic organ (ROSS & UNZICKER, 1977; SCHEFTER & UNZICKER, 1984; SCHEFTER, 2005). However the so-called neutral directional terminology remained frozen into the present day practice of species descriptions. We are turning back to the directional terms in spite of the unanimous voting to adopt NIELSEN's terminology (1957) by the participants in the First International Symposium on Trichoptera in Lunz am See, Austria (VSHIVKOVA, 2006). It is the time to use again the appendicular terminology reinforced by the newly discovered stimulatory and sensory functions in sexual selection, as well as by primordial groundplan reconstruction. We have to calculate and bear in mind its balance between possible limits, misuses and advantages.

New arguments of multiple stimulatory and sensory functions

The sensory and stimulatory roles of particular genital structures have been largely ignored, although these may provide an insight into the genital diversity processes driven by sexual selection. Insect terminalia bear setae (*sensilla trichoidea*) of various shapes and lengths together with several other types of sensilla (*sensilla chaetica*, *squamiformia*, *basiconica*, *coeloconica*, *ampullacea*). They are innervated mechanoreceptors and chemoreceptors. The sensilla on the terminalia function both in courtship, copulation and later in fertilization. However other male cuticular structures, like scales, microtrichia, acanthae, variously formed spines, sclerites and processes, occurring on insect terminalia are not innervated, but could stimulate innervated female receptors. Any fillips, flanges, blades, sclerites, intricate hooks, barbs, tufts, spines, microtrichia, surface corrugation, titillators, inflationary membranous structures may perform sensory and stimulatory functions in various processes of attraction, courtship, copulation, insemination and fertilization. The sexual selection hypothesis has been formulated only recently (ARNQVIST 1997, 1998) who discovered only a few mechanisms as to how these particular structural elements function. There is evidence for sexual selection acting on sclerites found frequently in the distal portion of the aedeagus. The function of these sclerites of various forms appears to play a role in the placement of the aedeagus within the female reproductive tract or in stimulation of the female (SIROT, 2003). Mechanosensory sensilla on diverse structures of the male genitalia have species-specific effects on mating position and on courtship success. Ablation of a single pair of bristles on the genital claspers halved homotypic mating success, and unilateral ablation produced a contralateral asymmetry in the mating posture of *Drosophila* (ACEBES & al. 2003). The

mechanism of rival sperm removal directly by males could be replaced by the stimulation of sensilla-bearing sclerite of female to eject rival sperm indirectly (CORDOBA-AGUILAR, 1999). The ejection mechanism itself could be controlled by the production and fit of male sex peptide and female sex peptide receptors (YAPICI & al. 2008). Coevolution between harmful spiny male genitalia and female resistance in counteradaptation by reinforced connective tissue in the copulatory duct involves more harmful genitalia with diverse spine patterns in male and more robust copulatory tracts in female (RÖNN & al. 2007). Adaptation in one sex should be matched by counteradaptation in the other. In the published discussion following VAILLANT's (1974) lecture on the presence of genital spines so frequently developed independently in the phallic apparatus of many caddisfly taxa, there was no answer to the question as to what is the function of these diversely developed eversible spines on the intromittant phallic organ. Similarly the sexual selection hypothesis helps to explain the disputed old theory of polygenotypism operating in intraspecific competition (BOTOSANEANU, 1974). These diverse sensory mechanisms produce particular genital structures in the course of sexual selection and this enormous genital diversity helps us to describe unknown species rapidly and reliably. At the same time this diversity makes it difficult to homologue the structural elements of the genitalia. The terminology of complicated genital elements is further confused by homologous structures serving different functions in different taxa. In spite of the high functional diversity, frequent functional interchanges and substitutes, the four appendicular complexes have their basic, most characteristic and dominant functions: (1) clasping function of *gonopod* on the IXth segment, (2) sperm intromittant function of the *phallic organ* of segment Xth origin, (3) stimulatory function of *paraproct* and (4) sensory function of *cercus*, both are of XIth segment origin.

Segmentation of insect body

The arthropods have at least 18 body segments or somites (metameres in embryo) when segmentation is complete: (1) four cephalic, (2) three thoracic and (3) eleven abdominal have been documented. The somites are formed during the embryonic segmentation process always posterior to an unsegmented preoral region, the prostomium, just before the mouth and always anterior to a small terminal piece, the telson or periproct containing the anus (proct). On the podial region of the embryo paired hollow outgrowth of the body wall (ectoderm) appearing soon after the body segmentation. However when arguing about the evagination pattern of the embryo it is important to realise that various appendages suppressed evolutionary in the adult may not appear either in the embryo. Each body segment between the prostomium and the telson may develop a pair of appendages from this ectodermal paired hollow outgrowth. Segmental appendages containing an extension of mesoderm become differentiated into limb segments or podites, potentially movable on each other through the development of muscle in the mesoderm of the appendage. However the evolutionary advantage of the body segmentation became fully functional when it was followed by appendicular segmentation of the primitive limb. The primitive arthropod limb first became divided into a basis or coxopodite and a distal arm or telopodite and segmented further. Lobes may be developed on the appendages: outer lobes or exite, exopodite, inner lobes or endite, endopodite individually movable with muscles arising in the preceding parts of the limb shaft. In such a way the somites became equipped with movable and segmented appendages, and the evolution of segmented segmental

appendages has produced the highly modified appendages on the head (antennocular, mandible, maxilla, labium), on the thorax (legs) as well as on the pregenital (segment VIII of females), genital (segment IX) and postgenital segments (segment X and XI) of the insect terminalia. It is still not fully documented whether the periphallallic organs and the phallic organ are of true appendicular or non-appendicular origin. However we assume that compartmentalization and structural development of abdominal segments simply copy the evolutionary pattern of the cephalic and thoracic segments.

Abdominal terminalia

"Insect terminalia" is a neutral term for the genitalia. The terminalia are the apical abdominal parts of the insect comprising the pregenital segment VIII, genital segment IX and postgenital segments X and XI if present. The aperture of the male genital duct appears to be always on the posterior part of segment IX, and the alimentary canal opens as the anus (or proct) at the end of the terminal segments X or XI. Some authors prefer to call the genitalia as insect terminalia, because varying parts are involved with reproduction. The insect terminalia or external genitalia is composed of periphallallic (gonopod, cercus, paraproct,) and phallic (phallic organ) structures.

Unmodified pregenital segment VIII. Segment VIII is the last typical abdominal segment with a separate tergum and sternum. Its posterior border frequently overlaps segment IX. As a result, the highly modified genital segment IX is partially or entirely concealed by segment VIII. Compared to abdominal segments I-VII the pregenital segment VIII is modified, but slightly. Both its tergum (*Limnephilidae*) and its sternum (*Protophilidae*) could be modified developing a middorsal incision or posterodorsal extension often covered with setae, bristles or pegs forming a setate/spinate area.

Modified diverse genital segment IX. The ninth abdominal segment developed as a genital segment, the gonosomite. The first highly modified segment on the insect terminalia, it is almost always in a single piece; not divided into tergite and sternite, forming a more or less complete annulus; the jaw-like configuration in *Dipseudopsidae* and *Psychomyiidae* being secondarily divided into tergite and sternite; in *Polycentropodidae* the dorsum is absent or much reduced, virtually absent. The primary external genital organ of male *Trichoptera*, the phallic apparatus is located usually medially on the venter or in the *Psychomyioidae* superfamily highly near the dorsum of the ninth abdominal segment. Accessory genital structures or periphallallic organs may be present on the periphery of the genital segment as well as on the pregenital or postgenital segments. Generally the ninth sternum is the male subgenital plate "hypandrium", but often the external plate beneath the male genital apparatus is the eighth or even the seventh sternum. Ventrally, it bears the gonopods. The development of genital segment IX is forced by its structural adaptation to special functions in the lock and key mechanism of the reproductive isolation or in the stimulatory and sensory role of sexual selection. The theory of reproductive isolation and more recently the theory of sexual selection try to explain the high diversity of the genital segment.

Reduced postgenital segment X. This is a composite structure, sensu lato it comprises also the vestigial sclerous or membranous elements of segment XI. It forms frequently a complex of segment X sensu stricto, and the vestigial cercus and paraproct of the eleventh segment. It is highly varying in shape, less pigmented, frequently semimembranous or membranous, nearly always narrower than segment IX. Its ventrum usually concave and partly encloses the phallic

organ, sometimes forming a functional tube around it. This is why it was known under the names of "dorsal plate", "penis cover", "upper penis cover". Frequently the sclerites of segment X are continuous with that of segment IX and difficult to recognise the boundary between them. Its possible fusion with the fragments of segment XI is represented by the paraproct. Its limb podites have been modified into the phallic organ. Cercus and paraproct of XI segment origin usually are associated with the periphery of segment X, seldom they are fused to its body.

Modified, reduced, fused or disappeared postgenital segment XI. If present, it represents the last true somite of the insect body. It is present in the embryos of the primitive insects with a well-developed metamere bearing the rudiments of cerci. It forms a normal annulus with tergal and sternal plates in adult *Protura*, but is more or less reduced in true *Insecta*, represented by epiproct and paraproct or almost entirely suppressed or fused to tenth segment in most of the *Holometabola*. When present it bears the cerci laterally and the anus (proct) at its apex. Its segmental plates are the dorsal epiproct and the lateral pair of paraprocts, both are present in *Rhyacophilidae* (NIELSEN, 1957; SCHMID, 1970).

Suggested appendicular and functional terminology

Based on the old arguments of comparative morphology as well as on the new arguments of multiple stimulatory and sensory functions but mostly in order to stimulate impetus to search homology and function in genital structures, we suggest and list here an appendicular and functional terminology. This is an old terminology. The terms were widely applied or are still consequently used by some workers (Neboiss, Morse and Johanson) in species descriptions. Due to the unresolved and single-sided dispute raised mostly by Schmid, we are steadily returning back to use the anatomical directional terminology, in spite of the tremendous contribution produced by Schmid himself to speed progress in appendicular and functional terminology. Right, it anatomical directional terminology is more neutral and very comfortable, but has no any stimulus to search and understand homology and function. Using this neutral directional terminology without understanding the origin and function of genital structural elements, our species descriptions remain less stable. If we use an appendicular and functional terminology, we create at least a perspective of provoking search to understand homology and function.

Gonopods

Instead of inferior appendages

This terminology assumes the appendicular origin of the gonopods as limb podites of the ninth genital segment. Gonopods consist of two segments representing the possible plesiomorphic state present in *Amphiesmenoptera* (IVANOV, 2005): the basal, proximal coxopodite (gonocoxite) and the apical, distal harpago (gonostylus, stylus). In many forms the two segments are jointed by several possible processes (NIELSEN, 1957): (1) by reduction of harpago, (2) by fusion of the two joints, (3) by fusion of the basal coxopodite with segment IX. Clasper is also a frequently used term (ROSS, 1938) referring to its main clasping or grasping function during copulation. In true limnephilids the gonopods often strongly reduced, single-segmented, and fused with segment IX. Its clasping function is taken over and performed by hooked paraproct or partially also by cerci (VSHIVKOVA, 2006). The two appendages of the gonopods are seldom separate (*Rhyacophila*) from each others. They are usually united at least by a membrane, but more frequently by an

unpaired sclerite, the basal plate, located at the bottom of the genital chamber.

Phallic organ

Instead of penis or aedeagus

Here we cite the appendicular nature of the phallic organ, as the limb podite of the tenth postgenital segment, although its appendicular origin is less documented and most disputed. According to this view the phallic organs similarly to the cephalic and thoracic podial segments are specially modified segmental appendages, but on the ninth or tenth abdominal segments. The great structural diversity is a delight of taxonomists, but despair of morphologists to homologise or to induce a common root either of primary phallic lobe (non-appendicular) or limb (appendicular) origin (SNODGRASS, 1957). The phallic organ has the intromittent function delivering sperm during copulation.

Paraproct

Instead of *intermediate appendages*

The definite paraproct is a paired lateral sclerite of the eleventh segment in certain primitive insects, near the anus. Paraprocts are frequently applied in higher insects to sclerites of doubtful homology in similar position on the eleventh or on the fused tenth and eleventh segment. We have to consider that the eleventh abdominal segment is frequently fused with the tenth segment. Paraprocts are a somite structure of the eleventh postgenital segment. A definite and complete eleventh segment is absent in the adult of most insect orders and is represented only by highly modified or vestigial somite or podite structures. If present the epiproct may be indistinguishable from the tenth abdominal tergum, as these two terga are often fused in pterygote insects. Usually the eleventh abdominal sternum is represented apically by the paraproct.

In *Trichoptera* the paraproct is the modified vestigial eleventh segment, frequently fused with tenth segment and/or with the cerci. The paraproct is usually heavily sclerotized, less setiferous and performing accessory copulatory and stimulatory functions, or seldom grasping function like in *Limnephilidae*. It is more developed in *Rhyacophilidae*, but in most other forms traces of it can be found (NIELSEN, 1957). Well developed in most representatives of the *Psychomyioidea* superfamily and much reduced in some *Integripalpia* or highly modified in the *Limnephiloidea* superfamily. If present (*Rhyacophila*), the eleventh abdominal tergum is the epiproct, the apical segment of the abdomen. Paraprocts are located frequently above and besides the anal opening and above the phallic opening, the ventral parts can be fused forming a closed structure around the anal opening or sometimes around the phallic organ like the paraproctal subphallic sclerite in many species in the *Polycentropodidae* and *Dipseudopsidae* families. There are views however that epiproct and paraprocts do not represent the true eleventh segment due to the lack of muscle attachment. These parts of the body might be regarded as the telson having no segmental nature (IVANOV, 2005).

Cercus

Instead of *superior or preanal appendages*

ROSS (1938) has used the term cercus consistently instead of preanal or superior appendages. NIELSEN (1957) stated that cerci are scarcely present in any Trichopteron male. SCHMID (1998) declared that male Trichoptera do not have any cerci. However what is the origin of the pair of those setose processes which are present in basoventral or dorsolateral

rear-most "tail" position on the tenth segment in almost all caddisfly species, even if present only in a highly reduced form, like the setose surface of most hydropsychid species. Is it a neoformation? Why? Why is it not the modified and shifted or vestigial and transplaced podit of the eleventh segment? IVANOV (2005) recently stated that the superior or preanal appendages covered with numerous sensillae are probably homologues of cerci: (1) their dorsolateral position on the segment X and (2) their primeval sensory function support this homology; moreover (3) they are also present in the Permian *Amphiesmenoptera*.

Cerci (plural of cercus; from Greek *kerkos* = tail) are sensory appendages, frequently movable by indirect muscles, mostly tactile organ of podite origin on the eleventh segment, implanted typically in membranous areas between the bases of the epiproct and the paraprocts behind the tenth tergum. These sensory appendages are homologous to the jointed legs of the thorax. Cerci are modified in many insects either as clasping organs or as defensive pincers. In true limnephilids the clasping role is performed partly by the usually hooked paraproctal complex and by the cerci, being their gonopods are strongly reduced, single-segmented and fused with the posterior margin of segment IX. When the eleventh segment is highly reduced or modified the cerci may be displaced, shifted and frequently associated with the Xth segment. Embryologists agree that cerci arise in the embryo as limb rudiments on the XIth segment. Their connection to the Xth segment becomes more pronounced with the reduction of the eleventh segment or its union with the tenth segment.

Annotated genital terms

Here we summarise the genital terms and their state variables applied during our species descriptions mostly in the *Psychomyioidea*, *Hydropsychoidea* and less in *Leptoceroidea* superfamilies (OLÁH & al. 2006a; 2006b; 2007; JOHANSON & OLÁH 2007; OLÁH & al. 2008; OLÁH & JOHANSON 2008a; 2008b) This list of annotations still reflects a mixture of the anatomical directional and the appendicular functional terminologies.

Eight segment

1 The last typical abdominal segment with separate tergum and sternum. Both its tergum (*Limnephilidae*) and its sternum (*Protoptilidae*) could be modified developing a middorsal incision or posterodorsal extension often covered with setae, bristles or pegs forming a setate/spinate area.

Ninth segment

2 *IX segment* heavily sclerotized, fused annular. The caddisfly ancestor *Amphiesmenoptera* in the late Permian already had the IXth segment with fully obliterated pleurites of the fused annular segment (IVANOV, 2005). Longitudinal sutures might represent the ventral or dorsal borders of the pleurite. The articulated dorsal or ventral parts of the IXth segment in some Trichoptera are apomorphi characters. Such a condition may be present in the species of the *Hydromanicus truncatus* species group (OLÁH & JOHANSON, 2008). State variables: size, length, shape

3 *Tergum and ventrum* of IXth segment. The tergum or dorsum of IXth segment may be formed by the Xth segment and most part of the Xth segment is represented by proctal processes of the XIth segment (NIELSEN, 1967; SCHMID, 1968, 1970). Nevertheless the Xth segment we accept and use here until more studies demonstrate that it is in reality the XIth segment with doubled epiproct and paired paraproct. The *Hydromanicus truncatus* new species group,

the most primitive species group of the most primitive hydropsychine *Hydromanicus* genus has the fused IXth segment clearly divided by a well-developed suture into smaller dorsal and larger ventral parts. State variables: length, size, shape.

4 *Acrotergit*. Usually a narrow less pigmented, semimembranous preantecostal lip of the tergum, punctate with variously developed microtrichia, sometimes contrasting significantly from the heavily sclerotized antecosta and antecostal suture, sometimes reduced or divided in the middle. State variables: pigmentation, surface structure, size, shape.

5 *Antecosta with groove system*. Marginal circumferential or submarginal ridge on the inner surface of the anterior margin of the tergal, sternal or fused plate is developed from the primary intersegmental fold, on which the longitudinal muscles are attached with the external groove of the antecostal suture. This may form a groove pattern on segment IX. The true antecosta is the anterior submarginal or marginal ridge on the inner surface of the fused IXth segment. A complete skeletal strengthening ridge or rim system might be developed from and composed of three components. (1) The primary intersegmental folds accompanied on the surface by the antecostal suture, the external groove of the antecosta. Attached to the antecosta (2) variously developed dorsal and ventral longitudinal grooves may represent the seamed pleurotergal and pleurosternal lines. This may be also called as *secondary longitudinal sutures* and may be present on laterodorsal, lateroventral or shifted positions. The third component of this reinforcement system is (3) the sclerotised sutures or lines with various width and shape on the posterior margin of the IXth segment. This, if present might be the vestigial antecosta and sutures of the Xth segment. The skeletal reinforcement or brace pattern of FLINT (1983, 1991) is composed basically from the same components. In his system the anterior marginal or submarginal brace is the true antecosta, the dorsal and ventral brace may represent the pleurotergal and pleurosternal lines and posterior marginal or submarginal brace on the IXth segment could be some functional form of Xth antecosta. In this interpretation scheme, the dorsal suture of BUENO-SORIA and ROJAS-ASCENCIO (2004) on the apicodorsal margin of IXth segment along the boundary of IXth and Xth segment is the dorsolateral marginal suture of segment IX. This suture seems common in Mexican and Central American *Marilia* species although we have not detected it in any of the examined Oriental *Marilia* species. However it may have some relation to the lateroapical corner of the IXth segment. State variables: presence, visibility, width.

6 *Lateroapical corner* of IXth tergum. The sclerotized lateroapical region of the IXth tergum is frequently developed into a variously shaped roof-like plate overhanging the articulation of preanal appendages. This posterior area on the lateroapical corner of the IXth tergum is an important diagnostic character in many *Marilia* species. In hydropsychid species, it may develop into an enlarged setose lobe, seldom with the preanal appendages shifted anteriorly and merged with dorsocaudal setose area of the IXth segment or the dorsoapical setose lobe on Xth segment shifted anteriorly. State variables: size, shape, elongation.

7 *Median keel or ridge* on IXth tergum, longitudinal keel with flat and granulose upper side (NIELSEN, 1957). The fused and elongated terminal fusion of the two antecostae or rather as the dorsal side of segment IX may be formed by segment X. State variables: size, shape, length, width.

8 *Anterior margin* of IXth segment. State variables: straight, rectangular, rounded, triangular, irregular, arciform.

9 *Lateral ridge* anteriorly on segment IX, just ventral to the base of the preanal appendages continuous with the

posterior margin (*Banyallarga*). Might be developed from a secondary laterodorsal longitudinal suture: state variables: size, shape.

10 *Apical lobe* on posterolateral margin, *lateral process*, *intermediate process*, *side piece* of MOSELY (1939). A lateral bulge on the posterior edge of the segment and sclerotized on the median side also (NIELSEN, 1957). State variables: size, length, width, shape, proximity to clasper.

11 *Lateral flank* between preanal and inferior appendages on the posterior margin of the IXth segment additional to the apical lobe.

12 *Posterolateral strips* of segment IX. These extend from the posterolateral margins of the segment into the genital chamber and articulate or fuse with the corresponding pair of strips from the sclerotic phallic shield surrounding the phallobase (MORSE, 1975).

13 *Dorsopleural* and *ventropleural setae* with various density and length. State variables: number, length, shape of setal area.

14 *Posterior spine row* on IXth segment (mesolateral setae of SCHEFTER, 2005). State variables: complete, intermittent, homogenous, heterogenous

15 *Dorsoapical spiny lobe* or setose area on the IXth dorsum. Frequently the two lateral posterior spine rows meet on the dorsum and develop into a delineated blunt lobe with longer and stronger setae, seldom the preanal appendages of the Xth segment shifted anteriorly and merged with dorsocaudal setose area or with the setose dorsoapical lobe of Xth segment shifted anteriorly. State variables: fused, paired, bulged, elongated.

16 *Ventrocaudal spiny lobe* of MALICKY (1997) on the IXth ventrum, *ventral plate* of MOSELY (1939), *ventrodistal* or *posteroventral setae* of SCHEFTER (2005). A median plate or process developed backward on the ventrum of IX segment, bearing stout and stiff spines. State variables: length, width, rounded, cut.

17 *Articulation cavity* of inferior appendages: State variables: wide, narrow, membranous.

18 *Intersegmental depression* in lateral view between the IXth and Xth segments. State variables: shallow-deep, acute angled, triangled, quadrangulate, right angled, obtuse angled, stepping, sloping, filled.

Tenth segment

19 *Xth segment (dorsal plate, penis cover, upper penis-cover)* is a disputed complex of the fused tenth and eleventh segments. According to SCHMID (1968, 1970) the Xth segment is reduced in *Arctopsychidae* and the *preanal appendages* or *superior appendages* as well as the *intermediate appendage* is in reality the eleventh segment. The intermediate appendages of *Arctopsychidae* are homologous with the anal sclerite (doubled *epiproct*) of *Rhyacophila*, but there is no apical band or tergal strap (*paraproct*) of the *Rhyacophila* present. In many insects, the limits of the Xth segment are often difficult to determine due to the frequent union between the Xth and XIth segments. SCHMID suggested that the Xth segment disappeared in *Hydropsychinae* as well and this structure is the intermediate appendages of the eleventh segment partially desclerotized and under one another. State variables: size, shape, setose units.

20 *Suture system* of internal ridge or apodemes on Xth segment: transversal and longitudinal, frequently integrated into Y-like suture system. A suture (transversal) with a corresponding internal ridge runs along the anterior dorsolateral area of the Xth segment. Ventrally or laterally, it joins another suture (longitudinal) and the two sutures

together form the Y-like suture figure (NIELSEN, 1957). Frequently the longitudinal suture or in combination with the transversal suture delineates a glabrous unsetose shallow or sometimes deep cavity. This suture system may represent the intersegmental line between the highly reduced Xth and XIth abdominal segments (SCHMID, 1968, 1970).

21 *Cavity on Xth segment behind the transversal and above the longitudinal sutures* is frequently present in *Hydropsyche* and may be homologous with the less pigmented basal area behind the transversal suture in *Cheumatopsyche* and may represent the highly reduced part of the Xth segment.

22 *Unsetose mesocaudal lobe*. Distal continuation of the dorsomedian body of Xth segment, a tongue-like plate on the dorsoapical margin of Xth segment, present in *Cheumatopsyche*. State variables: protruded, shortened, upcurving, convex, concave.

23 *Lateral setose area* of SCHEFTER (2005). Remnant of the movable *preanal appendages*, *superior appendages*, *socii* or *cercus* of ROSS (1956) on Xth segment, distad of transversal suture. Cerci are generally closely associated with the Xth segment, but implanted typically in a membranous area between the bases of the epiproct and the paraprocts behind the Xth tergum, and present on the embryo as limb rudiments on the XIth segments (SNODGRASS, 1935). State variables: long process, wart, raised area, surface or diffuse: size, shape, location, elevation.

24 *Dorsoapical setose area, lobe or crest* on Xth segment, distad of transversal suture absent on *Cheumatopsyche*, present frequently on *Hydropsyche* as a *setose winglet* (BOTOSANEANU & MARINKOVIC-GOSPODNETIC, 1966) or paired or fused *setose dorsal crest* (SCHEFTER, 2005). May represent the doubled *epiproct* of the XIth segment. State variables: paired or fused process, lobe, ridge, crest, surface, diffuse or reduced.

25 *Ventroapical setose area, lobe, elevation or process* on Xth segment, *digitiform process* (BOTOSANEANU & MARINKOVIC-GOSPODNETIC, 1966), small ventral processes with distal pencils of setae (NIELSEN, 1957), dorsolateral apical extension (SCHEFTER, 2005). May represent, even if it is just a setose surface, the rudimentary *paraproctal process* of NIELSEN (1957) and BOTOSANEANU & MARINKOVIC-GOSPODNETIC (1966), distad of transversal and ventrad, distad or in continuation of longitudinal suture. State variables: paired process, lobe, ridge, surface, elevation, diffuse or fused.

26 *Spiny apices* of the ventroapical setose area, or hook formation, well developed in *Potamyia*.

27 *Dorsal interlobular gap* between unsetose *mesocaudal lobe* and setose *ventroapical lobes*, visible in dorsal aspect if present.

28 *Lateral interlobular gap* between the bare unsetose *mesocaudal lobe* and setose *ventroapical lobes*, visible in lateral aspect if present.

Gonopod

29 *Gonopod*, *inferior appendages* or clasper two-segmented (basal segment: *coxopodite*, terminal segment: *harpago*) with distinct or indistinct articulation.

30 *Coxopodite*, (*coxopodium*, *gonocoxa*, *gonocoxite*) first or basal segment of the gonopod: length, size, slender-stout, straight-sinuuous, dilated basad or distad.

31 *Harpago*, (multiple *harpagones*, *telopodium*, *telopodite*, *gonostyli*, *styli*, *harpagones*) second, distal or apical segment of the clasper: length, size, shape, slender-stout, blunt-tapering, bifid, bilobed.

32 *Pons coxalis* and *basal plate*. In *Trichoptera* the coxopodites are generally united with each other medially by a membrane or by a transverse bridge lying in the floor of the genital chamber or by a basal plate. From the bridge, a median process extends upward in the genital chamber wall to give support to the sheath of the aedeagus. In *Hydropsyche* the basal plate is separated by a narrow membranous stripe, which is thus paired, however an indirect sclerotic connection between the two appendages is established through the sclerotic walls of the phallocrypt, the *basal plate* situated at the bottom of the genital chamber and above the two appendages. The basal plate must be considered as an integrating part of the inferior appendages.

Phallic apparatus

33 *Phallic apparatus*. In the *Hydropsychidae*, the phallic apparatus is formed by the elongated phallobase representing the phallothea and the endothea without aedeagus and parameres, but with well-developed endophallus. The endothea is almost reduced, but producing various, sometimes curious forms of endotheal membranous and sclerotized processes subapical, dorsoapical or ventroapical. It is present and well-developed in the most primitive *Hydropsyche vasuomittra* species group. The sclerotized tube of the phallobase in some taxa is interrupted by a dorsal opening anterior of the distal margin and phallosclerites, or is not sclerotized apico-dorsally, and forms a trough-like structure. In some species of the *Hydropsyche newae* species group a pair of unsclerotized circular window opens around the middle of the horizontal section of the phallobase. Phallobase (enlarged "phallobase"): size, shape, obtuse-right-acute angled or simple or sinuate bend formed by the downcurving basal section of the phallobase, with or without dorsal trough-like structure.

34 *Phallocrypt*. The proximal end of the phallic apparatus is lowered into a usually very deep depression, the *phallocrypt*. The walls of the crypt may be membranous or variously sclerotized, the sclerotic part sometimes forms a ring or tube from which the aedeagus projects. In *Hydropsychidae* the ventral floor and lower lateral wall of the phallocrypt is variously sclerotized, whereas the roof is formed by the proximal part of the phallobase. The lateral sclerotizations are connected with the basal plate of the inferior appendages by a pair of strong sclerotic rods (NIELSEN, 1957) or struts (SCHEFTER, 2005). The term phallocrypt means only that part, which lies beyond the phallic apodeme. This is the triangular area delimited by the rods (ventral) and the attachment point of the rods (proximal) plus the attachment area along the base of the phallobase (dorsal and distal).

35 *Phallic apodeme*. A phallic apodeme is formed by the fusion of the proximal end of the phallus with the anterior part of the wall of the phallocrypt. The apodeme may be partly membranous, but typically it is sclerotized.

36 *Phallobase*. Outside of phallobase. Phallobase is formed by the phallobase and the endothea. Very commonly the distal part of the phallobase forms a fold about the base of the aedeagus and this fold is sometimes produced into a tubular sheath, the phallobase. In such cases the aedeagus may be reduced or entirely suppressed, like in *Hydropsychidae*, where the entire phallic tube is the phallobase and its lining is the endothea. In *Hydropsychinae* the endothea is highly reduced, producing various processes at the distal end of the phallobase.

37 *Angular subapical lateral projection*. A structural element characterising the phallobase in the *Hydropsyche*

pellucidula species cluster of the *Hydropsyche angustipennis* species group (OLAH & JOHANSON, 2008a). An angular tooth-like projection just below the cleft apex of the phallotheca visible both in ventral and dorsal view.

38 *Endotheca*. Membranous sleeve connecting the phallobase (phallotheca by SCHMID, 1979) and phallicata (or aedeagus), reduced in *Hydropsychinae*.

39 *Phallicata*. Distal part of the phallotheca; phallotheca without phallobase; in *Hydropsychinae* reduced to phallotremal sclerites according to ROSS & UNZICKER (1977).

40 *Endophallus*. Elongated atrium-like structure usually well visible on the KOH macerated phallic apparatus. A permanent internal phallic structure, sometimes an eversible sac or tube. The sperm duct or ejaculatory duct enters its content through the valve-like *gonopore*. The endophallus empties its sperm content into the female through the *phallotreme*.

41 *Gonopore*. External opening of the ejaculatory duct, usually concealed in the endophallus. Weakly sclerotized ring at the proximal end of endophallus, usually narrower than the endophallic tube or sac.

42 *Sclerous band of endophallus*. Visible usually on the ventral position of the endophallus as a more sclerotized band. In most of the genera, the apex of this sclerous band is widened and forms a small plate that articulates with the phallotremal sclerites. The opening of the phallotremal sclerites is controlled by hydrostatic pressure and its closing controlled by the contraction of a sclerous band well visible after NaOH maceration. The ventral thickening of the endophallus by NIELSEN (1957). A more sclerous ventral part of the endophallus, participating in the closing procedure of the phallotreme by contraction or retraction. It is within or forming part of the ventral portion of the endophallus. However in some species the sclerous band of endophallus developed on the dorsal wall. The internal lips of NIELSEN (1957) could be a more sclerotised apical ending of the sclerous band.

43 *Phallotreme*. The distal opening of the endophallus, the sperm content is discharged through this apical opening.

44 *Phallotremal sclerites* (median plate, inner lip of MCFARLANE (1976), internal lip of NIELSEN (1957)). These sclerites flanking the phallotreme, the distal opening of endophallus, usually strongly chitinized, dark brown. Its free position is fixed dorsally or apically, but slightly variable, depending on the hydrostatic pressure in the endophallus at the time of preservation. Inside position occurs when covered by sclerotized endothecal movable processes in *Cheumatopsyche*, *Hydropsyche asiatica* species group, *Hydropsyche unguolata* new species group, *Orthopsyche* or when the sclerotized endothecal process fuse to the end of phallotheca in *H. propinqua* and *H. angustipennis* species groups. The phallotremal sclerites may represent the phallicata of ROSS and UNZICKER (1977). At the most primitive condition the phallotremal opening is narrowed by a pair of small folds or slightly chitinised sclerites. This morphological configuration is the basal stage present in *H. vasoumitra* species group for the formation and evolution of phallotremal sclerites discovered and described in six stages in the *Hydropsyche hamifera* species group by MEY (2003). (1) The ventral side of the phallotreme became sclerotized forming a small, unpaired sclerite, the *phallotremal tongue* of *H. hamifera* species group with a short and acute prolongation towards the membranous tip of the phallic apparatus, reaching less than half the distance to the tip. This stage is characterised as the *polyacantha* clade. (2) The phallotremal tongue has reached about the tip and its base enlarged surrounding the phallotremal opening however with weak dorsal sclerotization. This stage present at *javanica*

clade. (3) The base of phallotremal tongue is fully sclerotized surrounding the phallotreme, as a result the flat and band-like tongue is broadly attached to the surrounding and always with bifid tip. (4) The membranous erectile lobe of the endotheca at the tip of phallic apparatus replaced by sclerotized part, deeply cleft apically and together with the phallotremal tongue in the middle gives the trifid tip of the phallic apparatus. (5) A small supapical process remaining membranous on the lateral side. The base of these membranous appendages is always situated distally from the phallotreme. The apical spines of the rectile lobes shifted to the tip of the subapical appendages and directed proximad. The phallotremal tongue narrowed, but still broader than lateral lobes and with bifid apex. These characters are found at *H. calawiti* clade. (6) The subapical membranous appendages shifter further basad behind the phallotreme constituting the second pair of endothecal appendages. The trifid tip of the phallic apparatus is entirely sclerotized. The phallotremal tongue is scarcely broader than the lateral lobes. This stage constitutes the *hamifera* clade of the *H. hamifera* species group.

45 *Ventromesal subapical keel or hook*: usually a median ventrally flattened plate or hook situated subapical on the phallotheca.

46 *Terminal structures* of the phallotheca. These are the sclerotized and membranous endothecal processes and phallotremal sclerites. Apical, dorsolateral, dorsomedian and ventral membranous endothecal processes, appendages, lobes and lobules at the tip of the endotheca. Associated corrugations, microtrichia, reticulations, spicules, membranous spicule pockets, scattered spicules, spines, spurs and comutes are associated with these endothecal membranous appendages (ROSS & UNZICKER, 1977).

47 *Endothecal processes*. Parameres of NIELSEN (1957), SCHMID (1970) and MORSE (1975). However it is reasonable to follow SCHMID (1979) and retain the term parameres (the *titillators* of the old authors) for true appendages usually accompanying the aedeagus. The parameres are primitively paired, inserted on the endotheca in a lateral inferior position relative to the aedeagus and never present in a complete state when the aedeagus is lost. It is evident that the parameres are inserted on the endotheca, but many parts inserted on endotheca are not parameres. They are not true appendages and they are present when aedeagus and parameres have been lost by specialization and when the phallotheca and the endotheca have been secondarily elongated to replace the aedeagus. In *Hydropsychidae* several processes, membranous or sclerotized are produced apicad or subapicad by the endotheca with various names according to their position and to the stage of sclerotization. Their actual position, especially the position and direction of their well visible sclerotised structures of spines, spicules or corrugations are highly variable dependent on the stage of fixation after collecting the animal, whether protruded, intruded or intermittent.

48 *Sclerotised endothecal process*. [*endothecal valves*, *sclerotized lobes*, *outer lips*, *paramere* of NIELSEN (1957), SCHMID (1970), MORSE (1975), *apicolateral valves* or *motile apical valves* of SCHEFTER (2005)] Usually situated apicad. Flaplike and movable in *Cheumatopsyche* and *Orthopsyche* and fused to phallotheca in many species of the *Hydropsyche angustipennis* species group where only the phallotremal sclerites are movable. The fusion of the phallotremal sclerites with the sclerotized phallotheca is the synapomorphy of the *propinqua* and *angustipennis* species group and both evolved from descendants of the *newae* species group (ROSS & UNZICKER, 1977; MEY, 2005).

49 *Dorsal trough-like structure*: the sclerotized tube of the phallotheca is sometimes interrupted by a dorsal opening

anterior to the distal margin and phallotemal sclerites, or the sclerotized tube of phallotheca is not sclerotized apicodorsally and forms a trough-like structure.

50 *Endothecal spine-window*. In some species of the *newae* species group of the *Hydropsyche* genus a paired circular window, nested by a short and stout spine, is opened in the proximal part of the horizontal section of the sclerotised tube of the phallotheca both in dorsolateral or ventrolateral position. It does not seem very erectile, possibly just functioning as an accessory anchor or stimulator during copulation.

51 *Endothecal apical membranes*. When fully expanded their apices are frequently tipped by spines and spicules, usually not associated with phallotemal sclerites.

52 *Endothecal dorsal membrane*. Extrusible dorsal endothecal membrane surmounted with various spines or spicules anteriorly or distad of the phallotemal sclerites.

53 *Endothecal dorsolateral membrane* sometimes with dorsomedian lobes with spines and frequently with large anteroventral lobes with terminal spurs.

54 *Endothecal secondarily developed ventrolateral membrane*.

55 *Endothecal dorsomedian lobe* on endothecal dorsolateral membrane, unpaired, frequently with spine.

56 *Endothecal ventral membrane*. Usually slightly developed or protruded, frequently developed and visible subapically on *Potamyia* species from Madagascar.

57 *Endothecal membrane lobe*. In many species of *Orthopsyche* a ventral lobe of the endothea is produced apically and is divided into two or three membranous lobules.

58 *Ventral process*. A sclerotized ventroapical process. The phallotheca in some species is dorsoventrally furcated, with distally produced ventral sclerous process bearing eversible membrane or without this membrane.

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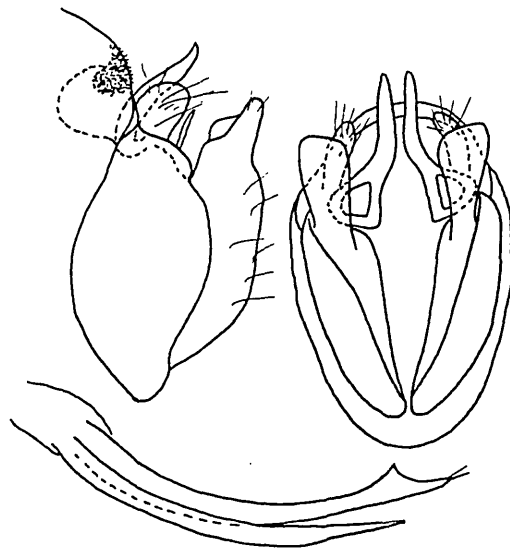
BRAUERIA (Lunz am See, Austria) 35:40 (2008)

Eine neue *Conсорophylax* – Art aus dem Piemont (Italien) (Trichoptera, Limnephilidae)

Hans MALICKY

Conсорophylax corvo n.sp.

Hellbraun, K  rper dorsal dunkler. Fl  gel br  unlich durchscheinend mit dunkler, gut abgehobenen Adern, Vorderfl  gelmembran verloschen hell gesprenkelt. L  nge eines Vorderfl  gels ♂ 18 mm. ♂ Kopulationsarmaturen: 8. Tergit dorsokaudal mit einem kleinen Dornenfeld. 9. Segment in Lateralansicht leicht bauchig, aber schlanker als bei den anderen Arten. Obere Anh  nge in Lateralansicht rund, mittlere Anh  nge in Lateralansicht lang, schlank, spitz und schr  g nach oben gerichtet. Untere Anh  nge in Lateralansicht   ber fast die ganze H  he des 9.Segments diesem eng anliegend, deutlich schlanker als bei den Verwandten, und dorsal in einen abgerundeten Lappen auslaufend; in Kaudalansicht lang, distal spatelf  rmig und den Dorsalrand des 9.Segments erreichend. Phallus in Lateralansicht schlank, mit einem subdistalen eckigen Vorsprung und zwei Endborsten. Parameren einfach, lang und spitz, ohne Borsten. – Durch die ungew  hnlich weit nach dorsal gezogenen unteren Anh  nge, deren Ende den Dorsalrand des Segments erreicht, und die einfachen, unbeborsteten Parameren von allen bisher bekannten sechs Arten der Gattung sofort unterscheidbar. – Der Name ist von Fundort (Torrente Corvo) abgeleitet.



Holotypus ♂: Italien, Piemonte, Briga Alta (Cuneo), Navette, Torrente Corvo, 1900m, 44  08'N, 7  43'E, leg. G. B. Delmastro, in meiner Sammlung.

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